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# WOOD ANATOMY OF *MACKINLAYA* AND *APIOPETALUM* (ARALIACEAE) AND ITS SYSTEMATIC IMPLICATIONS<sup>1</sup>

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## ABSTRACT

Wood anatomy was examined in both species of *Apiopetalum* (trees endemic to New Caledonia) and in two species of *Mackinlaya* (shrubs from Queensland, Australia), using light and scanning electron microscopy, to investigate their phylogenetic relationships and taxonomic position within Apiales. These genera share several wood features: small intervessel pits, ranging from 3 to 6  $\mu\text{m}$ ; both paratracheal and apotracheal (diffuse and diffuse-in-aggregates in *Apiopetalum* only) axial parenchyma; non-septate fibers; rays composed of mostly upright and square cells; and brown deposits in the vessels. Differences in wood structure between the genera appear to be related to habit. The results confirm recent molecular sequence data suggesting that *Apiopetalum* and *Mackinlaya* form a monophyletic group. Evidence from wood anatomy neither validates nor refutes the hypothesis that these two genera are intermediate between Araliaceae and Apiaceae and offers no clear indication of the group's phylogenetic position. Several wood characters (small intervessel pits, thick fiber walls, non-septate fibers) suggest a relationship with *Myodocarpus*, *Delarbrea*, and *Pseudosciadium*. No clear synapomorphies were found to support a sister relationship between *Apiopetalum* and *Mackinlaya* and core Apiaceae as previously suggested by Plunkett, nor between them and other Araliaceae. Helical thickenings on the walls of both ray and axial parenchyma, previously reported only once in *Trigonia* (Trigoniaceae), were observed in one sample of *M. macrosciadea*.

**Key words:** Apiales, *Apiopetalum*, Araliaceae, *Mackinlaya*, New Caledonia, phylogeny, Queensland, wood anatomy.

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The phylogenetic positions of *Apiopetalum* Baill. and *Mackinlaya* F. Muell. within Araliaceae have been difficult to assess using traditional approaches based on morphology. Recent studies using molecular data have provided new insights into their evolutionary relationships, but their exact placement remains unresolved. Five species of *Mackinlaya* (including *Anomopanax*) were recognized by Philipson (1979), extending from Queensland, Australia, through the Solomon Islands, Bismarck Archipelago, New Guinea, and Celebes to the Philippines (see also Philipson, 1951). *Apiopetalum* comprises

two species, both endemic to New Caledonia (Lowry, in prep.). *Mackinlaya* species are branched, sympodial shrubs with simple and palmately lobed or palmately compound leaves. *Apiopetalum* species are small trees, to ca. 6 m in height, and have exclusively simple leaves.

In most classification schemes proposed for Araliaceae (Bentham, 1867; Harms, 1894–1897; Viguier, 1906; Hutchinson, 1967; Tseng & Hoo, 1982; Takhtajan, 1987), *Apiopetalum* and *Mackinlaya* have been placed in a separate tribe Mackinlayeae, which has traditionally been distin-

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guished on only a few floral characters, primarily the presence of valvate, clawed petals. While Mackinlayeae have been recognized in nearly all classifications since that of Bentham (1867), this is more a reflection of sparse information on *Apiopetalum* and *Mackinlaya* than any real confidence in their relatedness. We do not consider similarities in the form and position of the petals as sufficient evidence to support the hypothesis that *Apiopetalum* and *Mackinlaya* form a monophyletic assemblage, and additional data are required to clarify their position within Araliaceae.

*Apiopetalum* and *Mackinlaya* have generally been regarded as most closely related to the well-defined group comprising *Myodocarpus*, *Delarbraea*, and *Pseudosciadium* (tribe Myodocarpeae), which is centered in New Caledonia (Lowry, 1986a, b). Although the monotypic genus *Pseudosciadium* was included in Mackinlayeae by Harms (1894–1897) because of its valvate, clawed petals, Baillon (1878, 1879) originally suggested that it was most closely related to *Delarbraea* and *Myodocarpus*. Baillon's initial interpretation has been supported by recent systematic studies, and data from the fruit structure (Lowry, 1986a, b) and wood anatomy (Oskolski et al., 1997) indicated that *Myodocarpus*, *Delarbraea*, and *Pseudosciadium* form a monophyletic assemblage. Results of recent phylogenetic analyses based on *matK*, *rbcL*, and ITS sequence data (Plunkett, 1994; Plunkett et al., 1996a, b, 1997, unpublished data) further support the hypothesis that these three genera form a distinct, basally branching clade within Apiales. These studies also suggest that *Apiopetalum* and *Mackinlaya* comprise a second, isolated clade within the order.

*Apiopetalum* and especially *Mackinlaya* resemble many Apiaceae in certain features, such as the presence of clawed petals, inflexed anthers in bud, a bicarpellate gynoecium, and a petiole base that forms a dilated sheath extending around the entire circumference of the stem (the latter two characters occur only in *Mackinlaya*). On this basis, Philipson (1970) and Rodriguez (1957, 1971) regarded *Apiopetalum* and *Mackinlaya* as possible intermediates between Araliaceae and Apiaceae, traditionally regarded as sister groups. In the molecular studies the exact position of the *Apiopetalum*–*Mackinlaya* clade within Apiales varies depending on the gene sequence and the type of analysis. In some trees, this clade is sister to Apiaceae (comprising subfamilies Apioideae and Saniculoideae, but excluding many genera traditionally placed in Hydrocotyloideae), whereas in other analyses the two genera are sister to the clade comprising the remaining Araliaceae.

Wood anatomical characters can provide useful complementary data for assessing relationships among the genera of Araliaceae, as shown by several previous studies (Oskolski, 1994, 1995, 1996; Oskolski et al., 1997). Until now, no information on the wood anatomy for either *Apiopetalum* or *Mackinlaya* has been available. The present study surveys the wood anatomy of both species of *Apiopetalum* and two of the five species of *Mackinlaya*. The results are examined with regard to hypothesized relationships between these genera, as well as with *Myodocarpus*, *Delarbraea*, and *Pseudosciadium*, core Araliaceae, and certain woody Apiaceae (*Bupleurum*, *Heteromorpha*, *Steganotaenia*, *Myrrhidendron*, *Eryngium*, *Gymnophyton*, *Asteriscum*, and *Trachymene*).

#### MATERIALS AND METHODS

Most wood specimens examined were collected by the authors and G. M. Plunkett; one sample of *Mackinlaya macrosciadea* was provided by B. Hyland (CSIRO Division of Plant Industry, Atherton), and another was taken from a plant at the Sydney Botanic Gardens. Voucher herbarium specimens from New Caledonia are deposited at MO, NOU, and P, and from Australia at QRS and MO. For the following descriptions, in cases where multiple samples of a species were examined and a feature was seen in only a portion of the material, the corresponding collections are indicated in square brackets. Wood samples were taken from trunks in *Apiopetalum* (from a primary branch in *A. velutinum* [3854]), and from basal portions of stems in *Mackinlaya*.

Standard procedures for the study of wood structure were employed to prepare sections and macerations for light-microscopic (LM) studies (Carlquist, 1988). Specimens for scanning electron microscopy (SEM) were prepared according to Exley et al. (1977). Descriptive terminology and measurements follow Carlquist (1988) and the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989), except that for the diameter of intervessel pits the vertical dimension was recorded because it is a more constant feature than the horizontal diameter in taxa with opposite and scalariform pitting.

#### RESULTS

##### 1. *APIOPETALUM* (FIGS. 1–4, 8–12; TABLES 1, 2).

*Material studied.* *Apiopetalum glabratum* Baill.: NEW CALEDONIA, Mé Ori, 830 m, Lowry 3375; 850 m, Lowry 4798. *A. velutinum* Baill.: NEW CALEDONIA, Mt. Mou, 1080 m, Lowry 3854; 1160 m, Lowry 4700.



Growth rings absent in *A. glabratum* [3375] (Fig. 1) and *A. velutinum* [4700], and distinctly marked by diffuse-in-aggregates and marginal axial parenchyma forming tangential lines and narrow bands near their boundaries (Fig. 2) in other specimens.

Vessels rounded to slightly angular in outline, narrow to moderately wide (tangential diameter (36–)66–87(–152)  $\mu\text{m}$ ), mostly in radial multiples of 2 to 4, not numerous (11 to 26 per  $\text{mm}^2$  in *A. velutinum* [4700]; and 27 to 50 per  $\text{mm}^2$  in other samples). Vessel walls 2–7  $\mu\text{m}$  thick. Tyloses not observed. Vessel element length (320–)620–820(–1140)  $\mu\text{m}$ . Perforation plates simple (more than 50%), and scalariform with few bars (up to 18 in *A. glabratum* [4798]), and reticulate (Figs. 9 and 10), rarely double, in  $\pm$  oblique end walls. Intervessel pits alternate (Fig. 11), rarely opposite to scalariform, 3–5(–6)  $\mu\text{m}$  in vertical diameter, rounded or oval with lens- to slit-like apertures. Vessel-ray and vessel-axial parenchyma pits with distinct borders; similar to intervessel pits in size and shape (mostly scalariform in *A. glabratum* [4798]), or unilaterally compound (horizontally to vertically elongated pits on the ray cell walls about 2 to 5 pits on the vessel walls), with lens- to slit-like apertures surrounded by shallow, groove-like wall sculptures (Fig. 12). Helical thickenings absent.

Vasicentric and vascular tracheids not observed.

Fibers libriform, thick- to very thick-walled (5–22  $\mu\text{m}$ ), non-septate, with few simple to minutely bordered pits with slit-like apertures in radial walls.

Axial parenchyma scanty in *A. glabratum* [3375] and *A. velutinum* [4700], somewhat more abundant in other specimens, both paratracheal (appears mostly as solitary parenchyma cells in *A. glabratum* [3375] and *A. velutinum* [4700], or incomplete parenchyma sheaths near vessels in others) and apotracheal (diffuse in *A. glabratum* [3375] (Fig. 1) and *A. velutinum* [4700], diffuse-in-aggregates or marginal parenchyma (Fig. 2) in both other specimens). Strands composed of (2)3 to 5(7) cells.

Rays (3)4 to 6(10) per  $\text{mm}$ , uni- and multiseriate, mostly 3 or 4 cells wide in *A. velutinum* (Fig. 4), and 4 or 5 cells wide in *A. glabratum* (Fig. 3) (up to 8 cells wide in *A. glabratum* [4798]). Ray height commonly exceeding 1 mm in *A. glabratum* (up to 2.9 mm high in *A. glabratum* [4798]), and usually less than 1 mm in *A. velutinum*. Multiseriate rays formed mostly by square and procumbent cells (the latter more numerous in *A. velutinum*), with 1 to 3 (up to 6) marginal rows of upright cells, and usually with sheath cells of square to upright shape. Uniseriate rays composed of upright cells, rarely with some solitary square and procumbent cells. Pits on tangential walls of ray cells rounded and oval, very small (1–2  $\mu\text{m}$  diam.). Radial canals absent.

Crystals (appearing mostly as a combination of few (1 to 3) large prismatic crystals with numerous small ones) common in ray cells (predominantly in square and upright ones) in *A. glabratum* [4798] and *A. velutinum* [4700], and in young parts of stem (near the pith) in *A. velutinum* [3854] (Fig. 8), occurring rarely in *A. glabratum* [3375]. Crystals present also in non-chambered axial parenchyma cells of *A. velutinum* [3854]. Brown and yellow deposits contained in a few vessels in both species examined.

## 2. *MACKINLAYA* (FIGS. 5–7, 13–16; TABLES 1, 2).

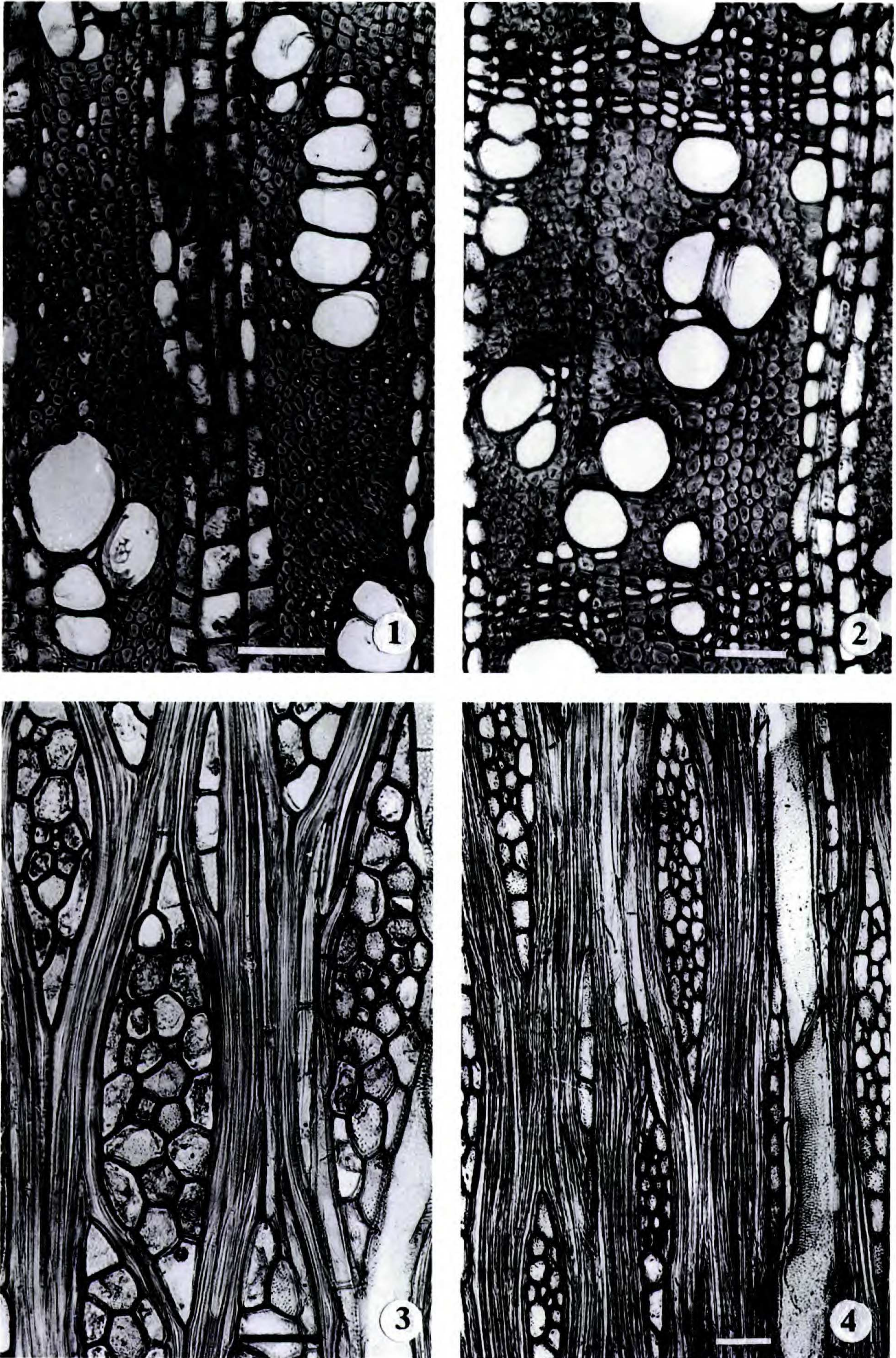
*Material studied.* *Mackinlaya confusa* Hemsl.: AUSTRALIA. Queensland: Bellenden Ker, 700 m, *Plunkett 1512*; Longlands Gap, 1120 m, *Plunkett 1520*; Isabella Falls, ca. 30 km NW of Cooktown, 180 m, *Plunkett 1549*. *M. macrosciadea* (F. Muell.) F. Muell.: AUSTRALIA. Queensland: without precise locality, 1100 m, *Hyland 15281*; Tolga, 800 m, *Plunkett 1497*; Gillies Lookout road, *Plunkett 1526*; cult. in Sydney Botanical Garden (NSW 208585), voucher for original collection: *Weston et al. 938* (AUSTRALIA. Queensland: Bellenden Ker, Mt. Bartle Frere; deposited at NSW).

Growth rings absent or  $\pm$  distinct (Fig. 5), marked by lines of marginal parenchyma.

Vessels rounded, very narrow (tangential diameter 9–31  $\mu\text{m}$  in *M. macrosciadea* [15281] and 20–52  $\mu\text{m}$  in other samples), not numerous (20 to 44 per  $\text{mm}^2$  in *M. confusa* [1512 and 1520]), to rather numerous (40 to 72 per  $\text{mm}^2$  in *M. confusa* [1549] and *M. macrosciadea* [1526 and 938], to 70 to 107 per  $\text{mm}^2$  in *M. macrosciadea* [1497 and 15281]), solitary and in radial multiples of 2 to 5 (up to 17 in *M. macrosciadea* [15281]). Vessel walls 2–5(–8)  $\mu\text{m}$  thick. Tyloses not observed. Vessel element length (270–)520–770(–1024)  $\mu\text{m}$ . Perforation plates scalariform with few (up to 14) bars and also rarely simple in *M. confusa* (observed in *M. confusa* [1549] only), or mostly simple (Fig. 14) and sometimes scalariform with few (up to 6) bars (Fig. 13) in *M. macrosciadea*, occasionally reticulate, in oblique and horizontal end walls. Intervessel pits transitional to alternate (transitional ones more common in *M. macrosciadea* [1497 and 1526], and *M. confusa* [1512]), rarely opposite, 3–6  $\mu\text{m}$  in vertical diameter, rounded or oval with slit- to lens-like apertures commonly surrounded by shallow, groove-like wall sculptures (Fig. 14). Vessel-ray and vessel-axial parenchyma pits with distinct borders, similar to intervessel pits in size and shape, or unilaterally compound (then horizontally to vertically elongated pits on the ray cell walls corresponding to 2 or 3 pits on the vessel walls). Helical thickenings absent.

Vasicentric and vascular tracheids not observed.





Figures 1–4. Light micrographs of *Apiopetalum* wood. —1. *A. glabratum*, Lowry 3375, transverse section, axial parenchyma scanty paratracheal and diffuse. —2. *A. velutinum*, Lowry 3854, transverse section, growth rings distinct, axial parenchyma scanty paratracheal and rather abundant diffuse-in-aggregates tending to form long tangential lines on growth ring boundaries. —3. *A. glabratum*, Lowry 3375, tangential section, mostly 4–5-seriate rays with sheath cells. —4. *A. velutinum*, Lowry 3854, tangential section, mostly 3–4-seriate rays with sheath cells. Scale bar = 100  $\mu\text{m}$ .





Figures 5–8. Light micrographs of *Mackinlaya* and *Apiopetalum* wood. —5. *M. macrosciadea*, Hyland 15281, transverse section, growth rings absent, axial parenchyma scanty paratracheal and diffuse. —6. *M. macrosciadea*, Hyland 15281, tangential section, 1–3-seriate rays composed mostly of square and upright cells, multiseriate portions of some rays as wide as uniseriate ones and alternate with the latter. —7. *M. macrosciadea*, Weston et al. 938, radial section, helical thickenings on the inner walls of the ray cells (arrows). —8. *A. velutinum*, Lowry 3854, radial section, crystals (arrow) in a ray cell in the young part of the stem (near the pith). Scale bar = 100  $\mu\text{m}$ .



Table 1. Data on wood samples examined and anatomical characters of vessel elements in *Apiopetalum* and *Mackinlaya*.

	Radius of sample 1	Radius of pith 2	Length of vessel elements 3	Diameter of vessels 4	Percentage of solitary vessels 5	Maximum vessel number per group 6	Vessel frequency 7	Number of bars per perforation plate 8
<i>Apiopetalum glabratum</i> Baill., <i>Lowry 3375</i>	34	4	663 ± 15.5 (710-1350)	87 ± 2.6 (48-152)	21	8	35 (31-50)	0 (0-15)
<i>A. glabratum</i> Baill., <i>Lowry 4798</i>	41	3	651 ± 38.1 (320-1140)	74 ± 1.1 (56-92)	17	7	31 (27-32)	0 (0-18)
<i>Apiopetalum velutinum</i> Baill., <i>Lowry 3854</i>	15	4	782 ± 19.4 (570-1000)	66 ± 1.6 (36-104)	46	4	32 (30-49)	0 (0-16)
<i>A. velutinum</i> Baill., <i>Lowry 4700</i>	34	3	822 ± 41.0 (460-1140)	80 ± 2.0 (52-128)	57	4	19 (11-26)	0 (0-14)
<i>Mackinlaya confusa</i> Hemsl., <i>Plunkett 1512</i>	11	1	770 ± 29.0 (520-1020)	36 ± 0.8 (20-48)	22	6	33 (27-44)	7 (3-14)
<i>M. confusa</i> Hemsl., <i>Plunkett 1520</i>	9	1	607 ± 32.0 (370-920)	30 ± 0.8 (20-44)	23	5	25 (20-35)	7 (3-9)
<i>M. confusa</i> Hemsl., <i>Plunkett 1549</i>	9	1	718 ± 24.8 (530-960)	36 ± 0.7 (24-52)	10	11	50 (42-69)	4 (0-12)
<i>Mackinlaya macrosciadea</i> (F. Muell) F. Muell <i>Plunkett 1497</i>	9	2	635 ± 17.0 (460-820)	32 ± 0.9 (20-48)	9	11	82 (70-107)	1 (0-4)
<i>M. macrosciadea</i> (F. Muell) F. Muell <i>Plunkett 1526</i>	7	2	663 ± 16.2 (550-800)	33 ± 0.8 (20-48)	10	12	60 (47-72)	1 (0-6)
<i>M. macrosciadea</i> (F. Muell) F. Muell, <i>Hyland 15281</i>	5	1	572 ± 28.3 (270-810)	21 ± 0.6 (9-31)	8	17	95 (79-102)	0 (0-5)
<i>M. macrosciadea</i> (F. Muell) F. Muell, <i>Weston et al. 938</i>	6	1	518 ± 28.8 (330-770)	30 ± 0.8 (20-44)	25	5	52 (40-69)	0 (0-5)

*Characters:* 1, Radius of wood sample (mm); 2, Radius of pith (mm); 3, Length of vessel elements ( $\mu\text{m}$ ): average  $\pm$  standard error (minimum - maximum); 4, Tangential diameter of vessels ( $\mu\text{m}$ ): average  $\pm$  standard error (minimum - maximum); 5, Percentage of solitary vessel lumina; 6, The greatest number of vessels in a vessel group; 7, Vessel frequency (per  $\text{mm}^2$ ): average (minimum - maximum); 8, Number of bars per perforation plate: average (minimum - maximum).



Table 2. Anatomical characters of libriform fibers and ray parenchyma in *Apiopetalum* and *Mackinlaya*.

	Length of fibers 1	Width of rays 2	Height of rays 3	Number of uniseriate rays 4	Number of multiseriate rays 5
<i>Apiopetalum glabratum</i> Baill., Lowry 3375	1029 ± 25.4 (710–1350)	4.3/6	1.1/2.9	0.8 (0–2)	3.0 (2–5)
<i>A. glabratum</i> Baill., Lowry 4798	1267 ± 26.4 (970–1840)	3.8/8	1.1/1.9	0.7 (0–2)	4.0 (2–5)
<i>Apiopetalum velutinum</i> Baill., Lowry 3854	1196 ± 26.8 (920–1510)	3.8/6	0.8/1.2	1.2 (0–2)	3.6 (2–5)
<i>A. velutinum</i> Baill., Lowry 4700	1074 ± 23.1 (810–1390)	3.3/5	0.6/1.2	0.5 (0–1)	3.6 (2–5)
<i>Mackinlaya confusa</i> Hemsl., Plunkett 1512	1324 ± 28.3 (870–1610)	1.3/3	0.8/3.1	10.5 (7–15)	2.4 (1–3)
<i>M. confusa</i> Hemsl., Plunkett 1520	1293 ± 27.6 (870–1620)	1.3/3	1.4/3.6	14.0 (12–16)	2.5 (1–5)
<i>M. confusa</i> Hemsl., Plunkett 1549	1076 ± 32.2 (730–1530)	2.1/5	1.7/3.6	8.6 (6–12)	4.5 (4–6)
<i>Mackinlaya macrosciadea</i> (F. Muell) F. Muell Plunkett 1497	1022 ± 21.0 (730–1300)	2.2/6	1.1/2.6	7.2 (3–12)	4.7 (3–6)
<i>M. macrosciadea</i> (F. Muell) F. Muell Plunkett 1526	1045 ± 22.2 (780–1310)	1.6/4	0.9/2.1	10.2 (4–14)	4.2 (2–7)
<i>M. macrosciadea</i> (F. Muell) F. Muell, Hyland 15281	801 ± 15.3 (620–1040)	1.5/3	0.7/1.1	13.9 (6–21)	4.7 (2–8)
<i>M. macrosciadea</i> (F. Muell) F. Muell, Weston et al. 938	722 ± 24.0 (420–1060)	1.8/4	0.9/1.9	8.7 (4–11)	12.5 (10–14)

*Characters:* 1, Length of libriform fibers ( $\mu\text{m}$ ): average  $\pm$  standard error (minimum – maximum); 2, Width of rays: average/maximum number of cell; 3, Height of rays (mm): average/maximum; 4, Number of uniseriate rays per mm: average (minimum – maximum); 5, Number of multiseriate rays per mm: average (minimum – maximum).

Fibers libriform, thin- to thick-walled (walls 3–5(–8)  $\mu\text{m}$  thick), non-septate, with rather numerous simple to minutely bordered pits with slit-like apertures in radial walls.

Axial parenchyma scanty paratracheal (appearing as solitary parenchyma cells near vessels), diffuse, and marginal, sometimes forming interrupted tangential lines (Fig. 5) and narrow bands near boundaries of the growth rings. Strands composed of 3 to 6(7) cells. Helical thickenings rarely present (*M. macrosciadea* [938]) on inner walls of the axial parenchyma cells in contact with vessels (Fig. 15).

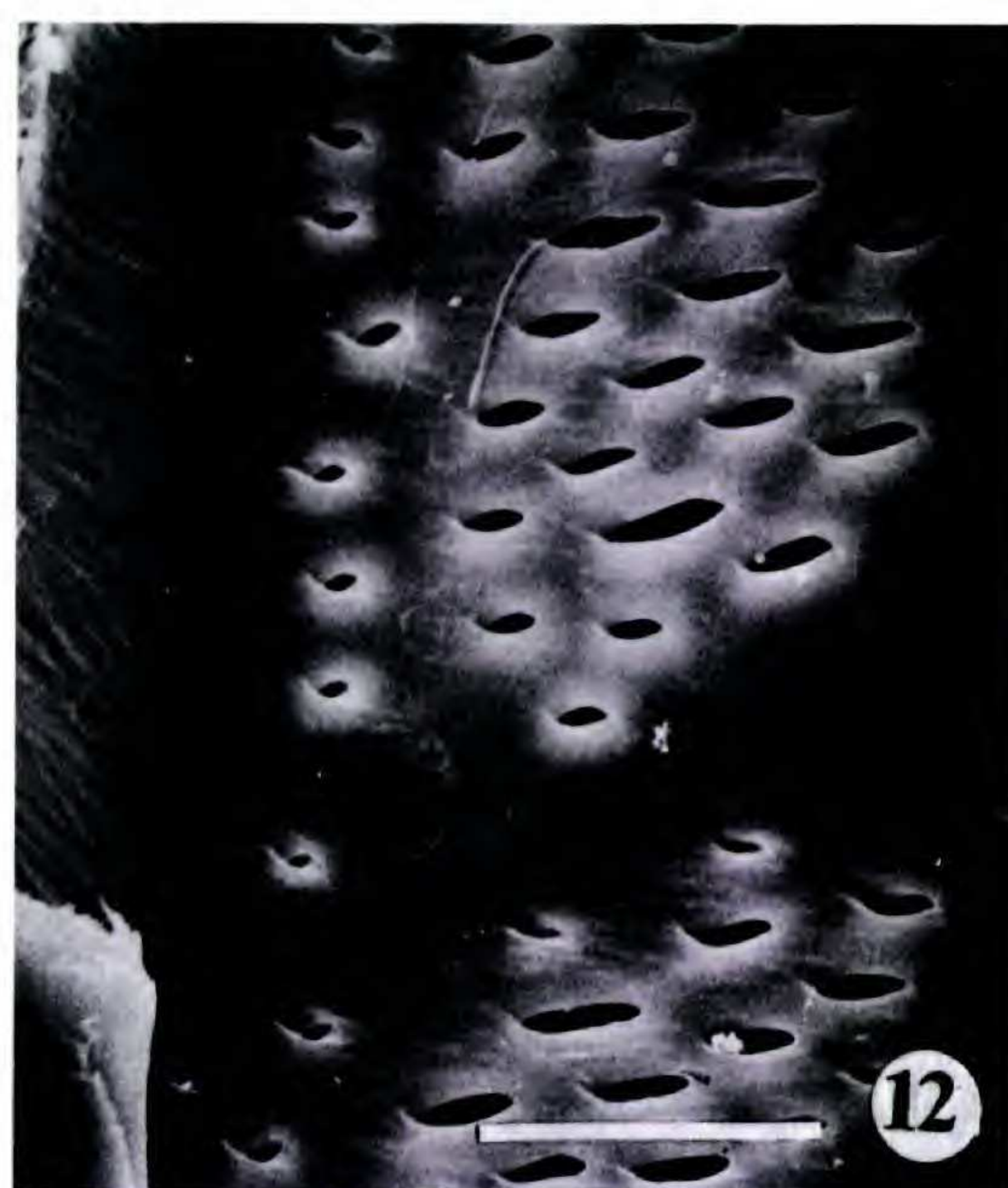
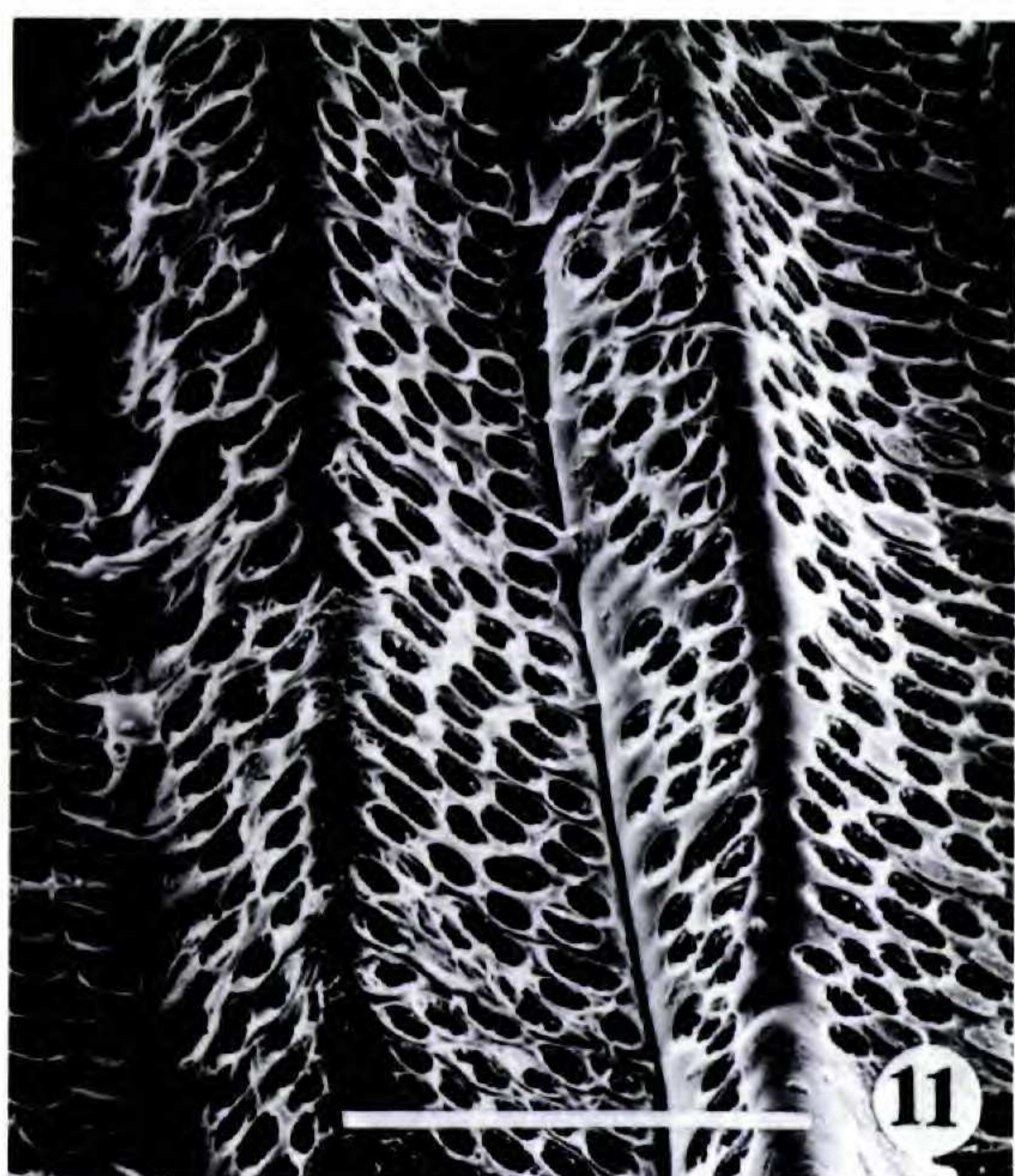
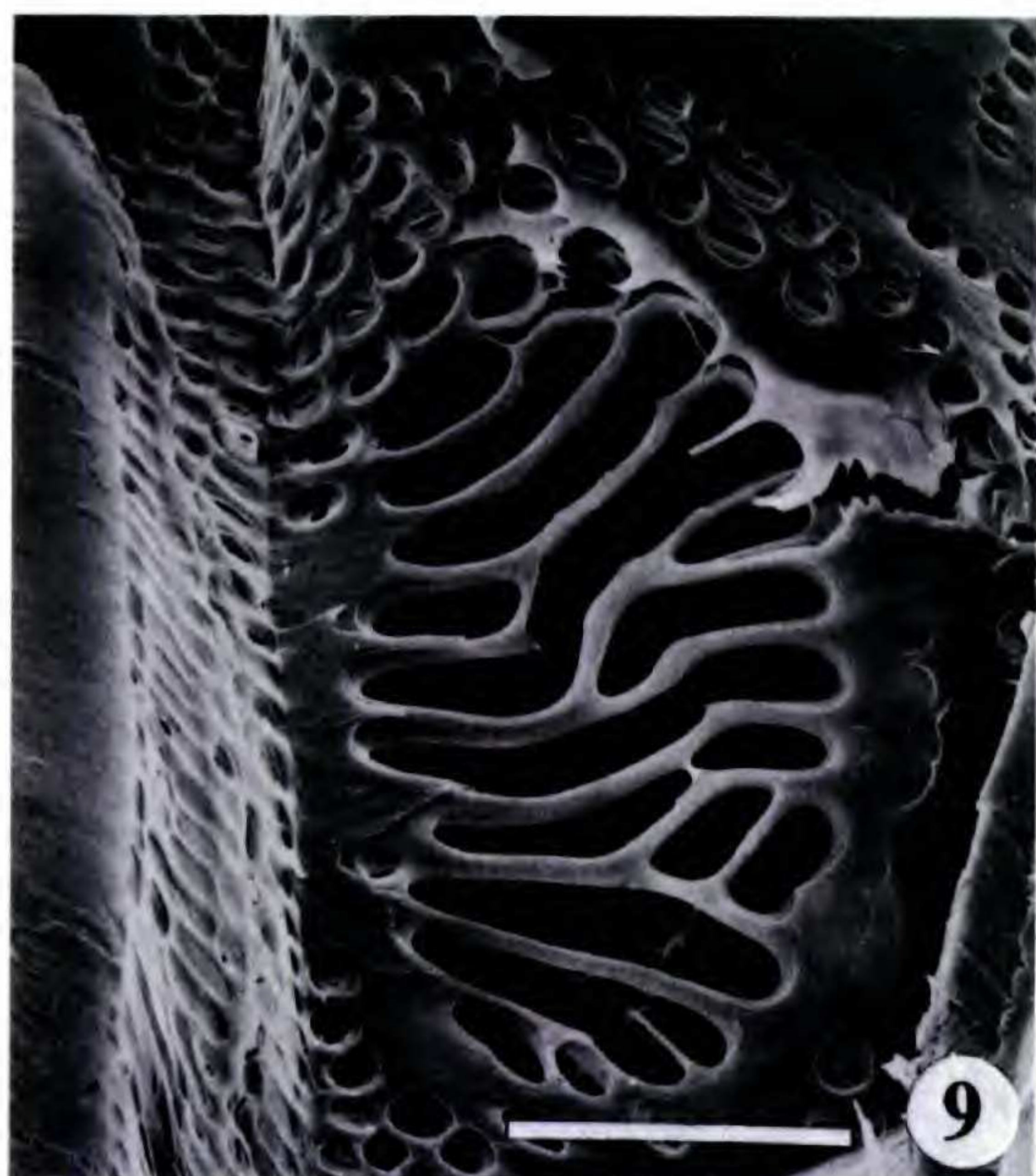
Rays numerous ((14)18 to 21(24) per mm), uniseriate and multiseriate of 2 or 3 cells in width in *M. confusa* [1512 and 1520] and wider in other samples (up to 6 cells in *M. macrosciadea* [1497]). Uniseriate rays more numerous than multiseriate ones in all samples except *M. macrosciadea* [938]. Ray height commonly exceeding 1 mm in *M. confusa* [1512 and 1549], and in *M. macrosciadea* [1497], and commonly less than 1 mm in other samples. Uniseriate rays composed of upright and few square cells. Alternation of uniseriate and mul-

tiseriate portions common in same ray. Uniseriate portions of multiseriate rays very long (up to 20 rows), formed by upright and solitary square cells, multiseriate portions usually as wide as uniseriate ones, composed of square and a few procumbent cells (Fig. 6). Pits on tangential walls of ray cells rounded and oval, very small (1–2  $\mu\text{m}$  diam.). Helical thickenings rarely present in *M. macrosciadea* [938] on inner walls of both upright/square and procumbent ray cells in contact with vessels (Figs. 7, 16). Radial canals absent. Crystals not observed. Brown and yellow deposits contained in a few to many vessels in both species examined, and also in cavities of many fibers and parenchyma cells of *M. macrosciadea* [938].

#### DISCUSSION

Very little variation was observed in wood structure within the *Apiopetalum* and *Mackinlaya* species examined. *Apiopetalum glabratum* differs from *A. velutinum* by higher and wider rays (Table 2). *Mackinlaya confusa* is distinct from *M. macroscia-*





Figures 9–12. Scanning electron micrographs of *Apiopetalum* wood. —9. *A. velutinum*, Lowry 3854, reticulate perforation plate. —10. *A. velutinum*, Lowry 3854, radial section, note one scalariform and two simple perforation plates. —11. *A. glabratum*, Lowry 3375, alternate intervessel pitting. —12. *A. velutinum*, Lowry 3854, vessel-ray pitting with lens-like apertures surrounded by shallow, groove-like wall sculptures. Scale bar in Figures 9–11 = 50  $\mu\text{m}$ , in Figure 12 = 20  $\mu\text{m}$ .

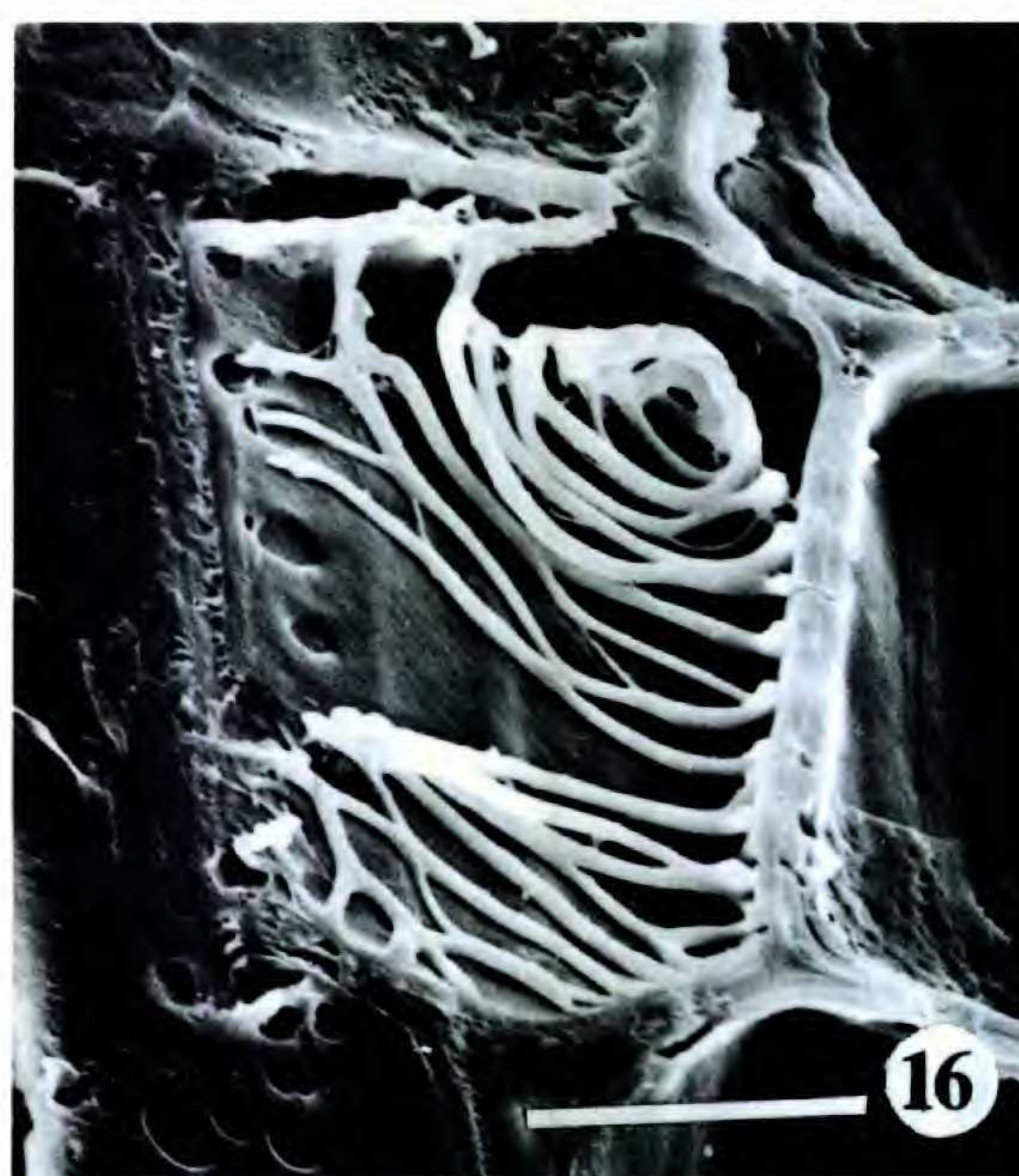
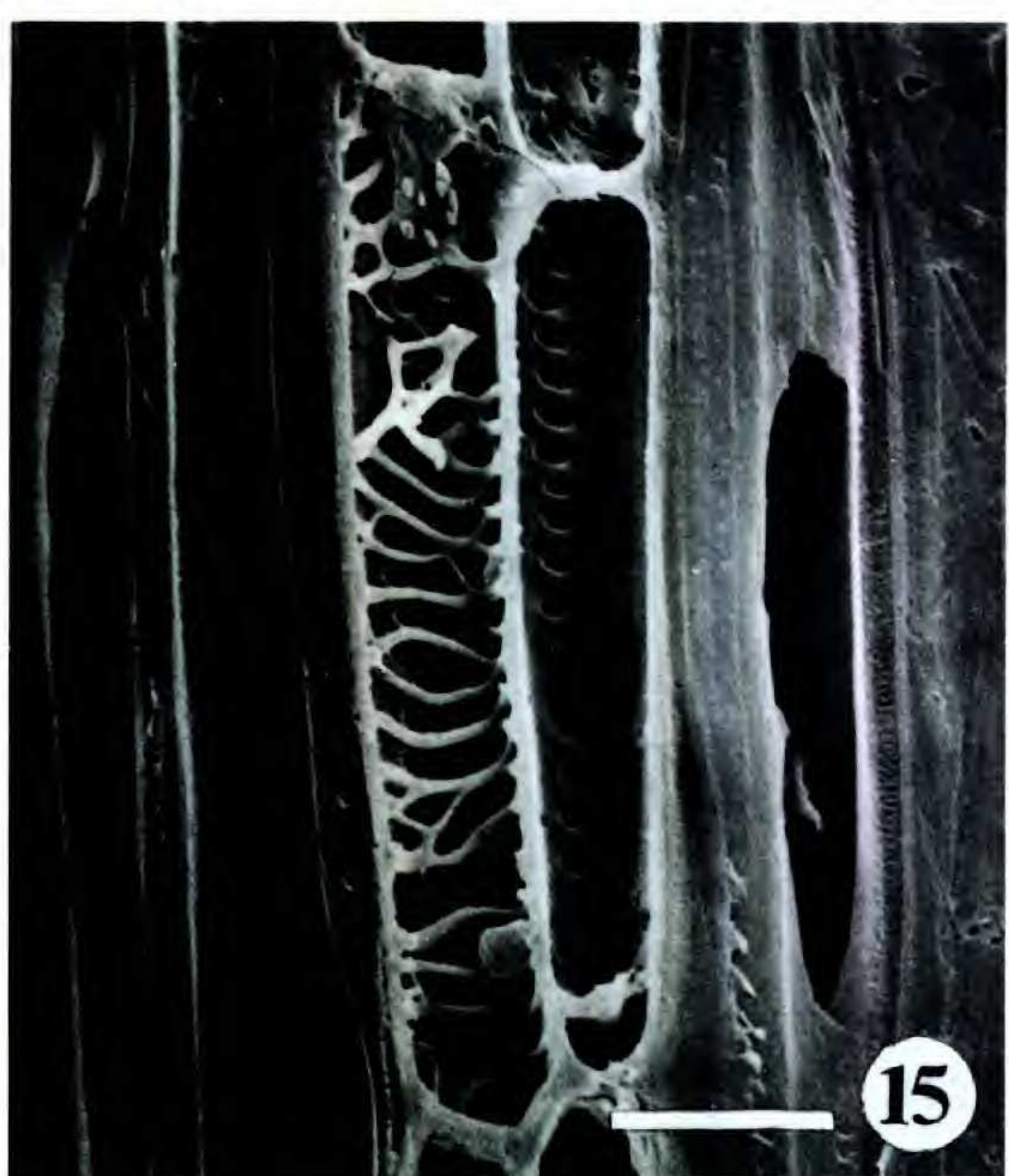
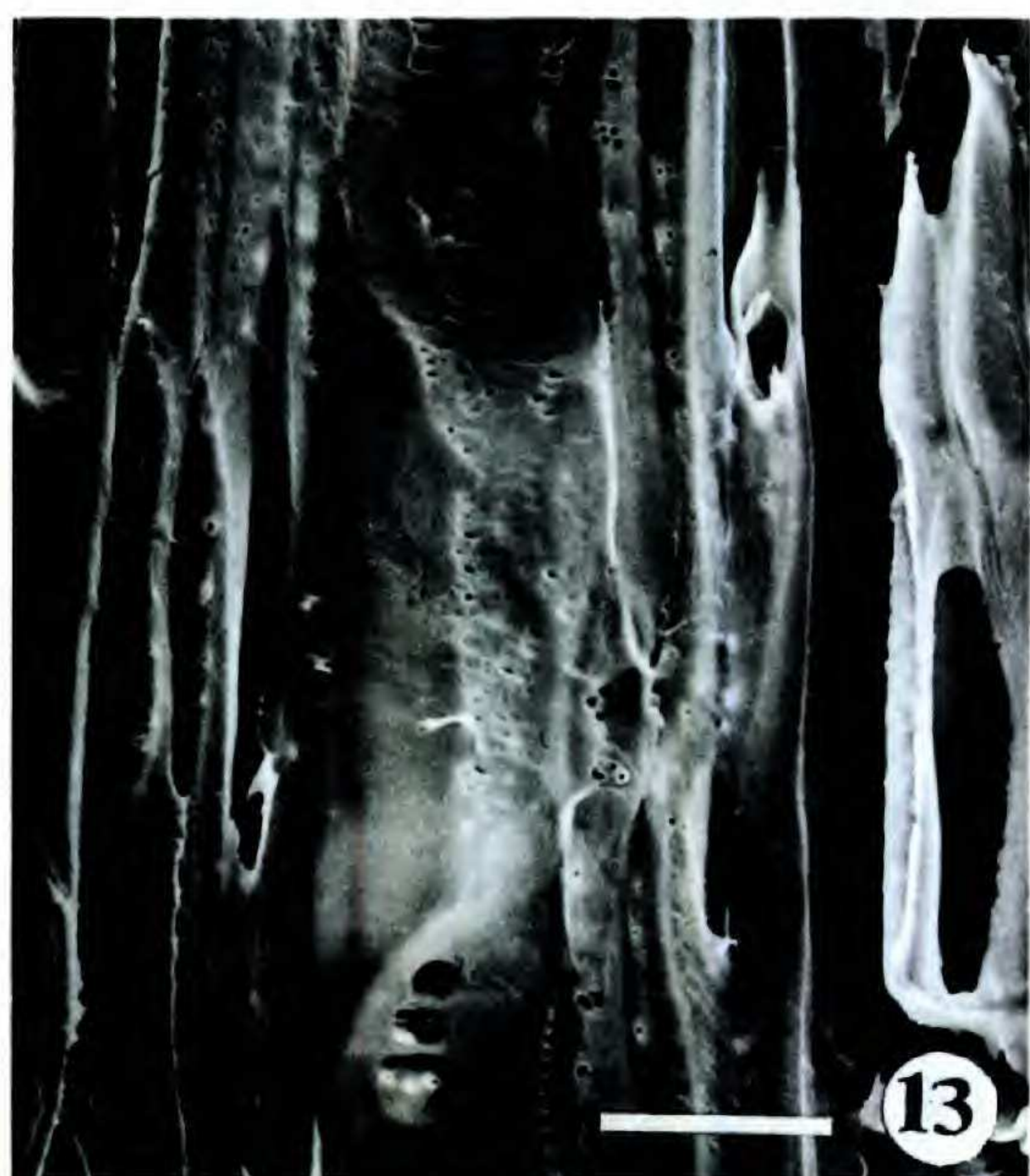
*dea* by the predominance of scalariform perforation plates with more numerous bars; it also has less numerous vessel lumina, but more samples must be studied before the importance of this character can be interpreted.

Helical thickenings on the walls of both ray and axial parenchyma were observed rarely in one sample of *Mackinlaya macrosciadea* [938] (Figs. 7, 15, 16). This feature generally appears in tracheal elements (vessel elements, vascular/vasicentric tracheids, fibers), and has also been reported very rarely in axial parenchyma of some Trigonaceae (Heimsch, 1942), Ancistocladaceae (Gottwald & Parameswaran, 1968), and Chrysobalanaceae (ter Welle, 1975). The presence of helical thickenings in ray cells appears to have been reported previ-

ously only for *Trigonía sericea* HBK (Heimsch, 1942: 133). In the sample of *Mackinlaya*, helical thickenings are found in parenchyma cells adjacent to the vessels.

*Mackinlaya* and *Apiopetalum* can be clearly distinguished from one another on the basis of their wood anatomy. Differences occur in several features, including narrower and more numerous vessels, thinner fiber walls, narrower and more numerous rays, the absence of diffuse-in-aggregates axial parenchyma, and the absence of crystals in the ray and axial parenchyma cells in *Mackinlaya* (Tables 1–3). The very narrow and relatively numerous vessels, and the 1- or 2-seriate rays found in *Mackinlaya* are probably correlated with the shrubby habit of the species studied and the correspondingly small di-





Figures 13–16. Scanning electron micrographs of *M. macrosciadea*, Weston et al. 938, wood. —13. Vessel element, scalariform perforation plates with few bars. —14. Simple perforation plate; small intervessel pits with slit- to lens-like apertures surrounded by shallow, groove-like wall sculptures. —15. Helical thickenings in an axial parenchyma cell. —16. Helical thickenings in a ray cell. Scale bar in Figure 13 = 50  $\mu\text{m}$ ; in Figures 14–16 = 20  $\mu\text{m}$ .

ameter of their stems. Other shrubby Araliaceae such as species of *Oplopanax* and *Astrotricha* (Oskolski, 1994, 1996) have mean values of vessel diameter and frequency, as well as of ray width, similar to those observed in *Mackinlaya*. Thickness of fiber walls, the type of axial parenchyma, and the occurrence of crystals in parenchyma cells appear to reflect relationships more than differences in habit or habitat (Oskolski, 1994, 1996), and could be of possible taxonomic value (Table 3).

Despite these differences in their wood anatomy, *Mackinlaya* and *Apiopetalum* also share a number of significant features. These include the small intervessel pits (3–6  $\mu\text{m}$ ), the occurrence of both paratracheal and apotracheal (diffuse and diffuse-in-aggregates, the latter occurring only in *Apiopetalum*) axial parenchyma, non-septate fibers, a pre-

dominance of upright and square cells in the ray composition, and brown deposits in the vessels. Although each of these characters has also been observed in other genera of Araliaceae and Apiaceae, their combined occurrence in *Mackinlaya* and *Apiopetalum* is notable for the order Apiales (Table 3) and supports the suggestion that these two genera are closely related. Diffuse and diffuse-in-aggregates parenchyma is found alone only in species of *Myodocarpus*, *Delarbrea*, and *Pseudosciadium*. Co-occurrence of both diffuse and paratracheal axial parenchyma is known only from three New Caledonian species of the pan-tropical genus *Schefflera* (Oskolski & Lowry, in prep.). All other representatives of Apiales examined to date have only a single parenchyma type. The co-occurrence of apotracheal and paratracheal axial parenchyma could



Table 3. Wood anatomical diversity in *Apiopetalum*, *Mackinlaya*, other Araliaceae, and selected woody Apiaceae. Noteworthy character associations are outlined in boxes. For character states co-occurring in individual samples, all are listed; "+" = character present; "-" = character absent; "+/-" = character intermediate between two contrasting states.

	Vessels narrow		Size of intervessel pits	Fiber wall thickness	Septate fibers	Axial parenchyma type	Ray type	Radial canals	Crystals
	1	2							
<i>Apiopetalum glabratum</i>	-	x	xxx	-	P, M, D, Da	IIA	-	+	+
<i>A. velutinum</i>	-	x	xxx	-	P, M, D, Da	IIA	-	-	+
<i>Mackinlaya confusa</i>	+	x	x	-	P, M, D	IIA	-	-	-
<i>M. macrosciadea</i>	+	x	x	-	P, M, D	IIA	-	-	-
<b>Other Araliaceae<sup>1</sup></b>									
<i>Myodocarpus</i>	+/-	x	xxx	+/-	D, Da	Ho	+	-	-
<i>Delarbraea</i>	+/-	x	xxx	-	D, Da	Ho	+	-	-
<i>Pseudosciadium</i>	+	x	xxx	-	D, Da	Ho	+	-	-
<i>Astrotricha</i>	+	x	x	-	P	Pm	-	-	-
<i>Dendropanax<sup>2</sup></i>	+/-	xx	x	+	P	IIB	+	-	-
<b>Woody Apiaceae<sup>1</sup></b>									
<i>Bupleurum</i>	+	xx	xx	?	P	IIB	-	-	-
<i>Heteromorpha</i>	+/-	?	x	?	P	IIB	-	?	?
<i>Steganotaenia</i>	-	?	x	?	P, M	IIB	+	?	?
<i>Myrrhidendron</i>	+/-	?	x	?	P	IIB	-	-	-
<i>Eryngium</i>	+/-	?	x	?	P	IIB	+	?	?
<i>Gymnophyton</i>	+/-	?	x	?	P, M	IIB	-	?	?
<i>Asteriscum</i>	+/-	?	x	?	P, M	?	-	?	?
<i>Trachymene</i>	+	?	x	?	P	IIB	-	-	?

**Characters:** 1, Vessel lumina narrow (diameter < 50 µm); 2, Size of pits of the intervessel pitting (x = up to 8 µm, xx = more than 8 µm in vertical diameter); 3, Libriform fiber wall thickness (x = thin, xx = thin to thick, xxx = very thick); 4, Presence of septate fibers; 5, Axial parenchyma types (P = scanty paratracheal, M = marginal, D = diffuse, Da = diffuse-in-aggregates); 6, Ray type (I, IIA, IIB = Kribs's (1935) types of heterogeneous rays, Ho = homogeneous I rays, Pm = "paedomorphic" rays (Carlquist, 1988), which are composed of square and upright cells only); 7, Presence of radial canals; 8, Presence of crystals in ray and/or axial parenchyma cells.

**Notes:** 1. Data on genera of Araliaceae other than *Apiopetalum* and *Mackinlaya* are from Oskolski et al. (1997) for *Myodocarpus*, *Delarbraea*, and *Pseudosciadium*; and Oskolski (1996) for *Astrotricha* and *Dendropanax*. Data on woody Apiaceae are from Rodriguez (1957), Metcalfe & Chalk (1950), Greguss (1959), and Schweingruber (1990). 2. Data on *Dendropanax* are presented as an example of the wood characters typical for most Araliaceae.



thus be regarded as an apomorphy for *Mackinlaya* and *Apiopetalum*.

Besides diffuse and/or diffuse-in-aggregates axial parenchyma, several other wood-anatomical features are also shared among *Mackinlaya*, *Apiopetalum*, and the assemblage comprising *Myodocarpus*, *Delarabrea*, and *Pseudosciadium*, such as the presence of small intervessel pits. This character occurs nowhere else within Araliaceae except in the Australian endemic *Astrotricha* (Table 3), which may also be a basally branching lineage of Apiales as indicated by recent molecular sequence data from ITS (Mitchell & Wagstaff, 1997; G. M. Plunkett, pers. comm.). However, the wood of *Astrotricha* differs strongly from that of *Mackinlaya* and *Apiopetalum*, notably in its axial parenchyma and ray types, and the presence of helical thickenings on the vessel walls (Oskolski, 1996). Species of *Mackinlaya*, *Apiopetalum*, *Myodocarpus*, *Delarabrea*, and *Pseudosciadium* also form very thick-walled non-septate fibers, which are unusual within the order. Each of these wood characters may be a synapomorphy within Apiales (Table 3), supporting the hypothesis of monophyly of the alliance that contains these five genera. They could likewise be symplesiomorphic in that they occur independently (but not together) in other groups within the order (Table 3), suggesting the possibility of parallel evolution. Resolving this issue is difficult at present because we lack sufficient data on wood features (especially the size of intervessel pits) for nearly all genera of woody Apiaceae.

These similarities notwithstanding, wood anatomy of *Mackinlaya* and *Apiopetalum* is nevertheless very distinct from that of *Myodocarpus*, *Delarabrea*, and *Pseudosciadium*. In addition to the co-occurrence of both paratracheal and apotracheal (diffuse and diffuse-in-aggregates) axial parenchyma, ray types also differ. In *Mackinlaya* and *Apiopetalum*, rays are heterogeneous, with both upright and square as well as procumbent cells; they are homogeneous with exclusively procumbent cells in the other genera. Furthermore, *Mackinlaya* and *Apiopetalum* have brown and yellow deposits in their vessels and lack radial canals. Wood anatomy thus supports the inclusion of these genera in a monophyletic Mackinlayeae (Table 3), and refutes the inclusion of *Pseudosciadium* (Baillon, 1878, 1879), which is most closely related to *Myodocarpus* and especially *Delarabrea* (Lowry, 1986a, b; Oskolski et al., 1997; Plunkett, 1998, unpublished data).

Using generally accepted trends in wood evolution (Bailey & Tupper, 1918; Frost, 1930a, b, 1931; Carlquist, 1988; Baas & Wheeler, 1996) to determine character polarity, several features are regarded as

plesiomorphic for *Mackinlaya* and *Apiopetalum*. These include predominantly scalariform perforation plates and relatively long vessel elements, whereas short vessel elements with exclusively simple perforation plates of woody Apiaceae (Metcalf & Chalk, 1950; Rodriguez, 1957; Greguss, 1959; Schweingruber, 1990) are regarded as apomorphic. Average vessel element lengths are 651–822  $\mu\text{m}$  in *Apiopetalum* and 518–770  $\mu\text{m}$  in *Mackinlaya* (Table 1), within the range seen in most other Araliaceae, which vary from 650 to 900  $\mu\text{m}$ . The lowest reported averages are 366  $\mu\text{m}$  in *Oplopanax horridum* (J. Smith.) Miq. and 374  $\mu\text{m}$  in *Eleutherococcus sessiliflorus* (Rupr. & Maxim.) S. Y. Hu, with the highest of 1339  $\mu\text{m}$  reported in *Schefflera gabriellae* Baill. (Oskolski, 1994, 1996; Oskolski & Lowry, in prep.). By contrast, vessel elements in *Apiopetalum* and *Mackinlaya* are distinctly longer than in woody Apiaceae, which have average values that are generally less than 400  $\mu\text{m}$ . A notable exception is *Heteromorpha arborescens* (Thunb.) Cham. & Schlecht., whose average vessel length reaches 502  $\mu\text{m}$  (Rodriguez, 1957). Wood features characteristic of *Mackinlaya* and *Apiopetalum*, such as the occurrence of diffuse and diffuse-in-aggregates apotracheal parenchyma types, small intervessel pits, and heterogeneous rays with distinct uniseriate portions composed of upright and square cells (Kribs's (1935) IIA type), have not been reported among the woody Apiaceae examined, including species of *Bupleurum*, *Heteromorpha*, *Steganotaenia*, *Myrrhidendron*, *Eryngium*, *Gymnophyton*, *Asteriscum*, and *Trachymene* (Table 3), among others (Metcalf & Chalk, 1950; Rodriguez, 1957; Greguss, 1959; Schweingruber, 1990).

Wood anatomical features thus confirm that *Mackinlaya* and *Apiopetalum* are closely related and occupy an isolated position within Apiales, as proposed by Plunkett (1998). However, wood characters neither validate nor refute the hypothesis that the two genera under study are intermediate between Araliaceae and Apiaceae (Philipson, 1970; Rodriguez, 1957, 1971), nor do they offer a clear indication of the group's phylogenetic position within the order. Based on current data, we cannot identify any reliable synapomorphies in the wood to support a sister relationship between the *Apiopetalum*–*Mackinlaya* clade and core Apiaceae (excluding most members of subfamily Hydrocotyloideae), as suggested by Plunkett (1998), nor between them and core Araliaceae (excluding *Myodocarpus*, *Delarabrea*, and *Pseudosciadium*). However, the study of wood structure is of limited use in assessing relationships between *Mackinlaya* and *Apiopetalum* and non-woody members of the *Mack-*



*inlaya* group, as defined by Plunkett (1998, pers. comm.), or between them and nearly all of the other genera of Apiaceae, which are likewise herbaceous. Several wood characters (small intervessel pits, thick fiber walls, non-septate fibers) do suggest a relationship between *Mackinlaya* and *Apiopetalum* and the alliance comprising *Myodocarpus*, *Delarbraea*, and *Pseudosciadium*, as previously hypothesized (Plunkett et al., 1996a, b, 1997).

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